Seasonal Movement of Brown Trout in a Southern Appalachian River

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Abstract.-Radio telemetry was used to evaluate the seasonal movement, activity level, and home range size of adult brown trout Salmo trutta in the Chattooga River watershed, one of the southernmost coldwater stream systems in the United States. In all, 27 adult brown trout (262-452 mm total length) were successfully monitored from 16 November 1995 to 15 December 1996. During the day, adult brown trout were consistently found in small, well-established home ranges of less than 270 m in stream length. However, 8 of a possible 18 study fish made spawning migrations during a 2-week period in November 1996. The daytime locations of individual fish were restricted to a single pool or riffle-pool combination, and fish were routinely found in the same location over multiple sampling periods. Maximum upstream movement during spawning was 7.65 km, indicating that brown trout in the Chattooga River have the ability to move long distances. Spawning brown trout returned to their prespawning locations within a few days after spawning. Brown trout maintained larger home ranges in winter than in other seasons. When spawning-related movement was deleted from the analysis, brown trout moved more on a weekly basis in fall than in summer. Brown trout were more active in fall and winter than in spring

and summer. Apart from spawning migrations, displacement from established home ranges was not observed for any fish in the study. Although summer water temperatures reached and exceeded reported upper thermal-preference levels, brown trout did not move to thermal refuge areas in nearby tributaries during the stressful summer periods.

Brown trout Salmo trutta exhibit strong site fidelity, often spending the majority of their lives within small, well-defined home ranges (Bachman 1984; Young 1994). Home range size may vary by season (Matthews et al. 1994), as brown trout move great distances in response to changes in temperature both in summer and during the fall spawning season (Clapp et al. 1990; Meyers et al. 1992: Hudson 1993). Brown trout also exhibit seasonal differences in diel activity (Eriksson 1978; Schulz and Berg 1992; Bunnell et al. 1998). Little is known about brown trout movement patterns in the southern Appalachians, where summer water temperatures often exceed levels considered stressful to brown trout (Elliott 1975; Garrett and Bennett 1995). Studies of brook trout Salvelinus fontinalis and rainbow trout Oncorhynchus mykiss in this region suggest that movement may be limited (Whitworth and Strange 1983; Ensign et al. 1990), although brown trout have been observed to seek thermal refuge during periods of extreme

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temperature in some studies (McMichael and Kaya 1991; Garrett and Bennett 1995). Investigation of the relationship between seasonal movement patterns and temperature could provide fisheries managers with a better understanding of the mechanisms influencing southeastern brown trout populations. In this study, we evaluated seasonal differences in the activity level, movement, and home range size of brown trout in the Chattooga River, one of the southernmost coldwater streams in the United States.

Study Site

The Chattooga River watershed covers an area of 720 km² in the headwaters of the Savannah River. The Chattooga River originates in southwestern North Carolina and flows south, forming the boundary between Georgia and South Carolina and terminating as a fourth-order stream in Lake Tugaloo. Over a course of 34 km, the river drops in elevation from 1,460 m to 1,275 m, forming a deep-sided gorge through crystalline bedrock. River morphology is dominated by bedrock ledge cascades, shallow (<0.5-m), high-gradient riffles, and deep (>0.5-m), low-gradient pools. Annual precipitation ranges from 177 to 229 cm, and flooding occurs frequently (USFS 1971). Our study was confined to the area between the North Carolina border and the bridge at South Carolina Highway 28, and included four tributaries: Reed Creek, King Creek, East Fork, and Bad Creek. The study area was selected so that there would be no barriers to brown trout movement for at least 5 km in either direction.

Methods

Thirty-four brown trout ranging from 262 to 452 mm total length were collected by electrofishing or hook and line over an 8-week period in fall 1995 (N = 15) and a 12-week period in spring 1996 (N = 19). Results are restricted to the movements of 27 brown trout found on consecutive sampling periods at least 30 d from the date of transmitter implantation. Transmitters were surgically implanted immediately after each fish was captured. As described by Bunnell et al. (1998), each fish was anesthetized, and an approximately 1.5-cm incision was made in the ventral surface of the abdomen. A radio transmitter was inserted into the body cavity with the antenna protruding through the incision. The incision was closed with three absorbable sutures. Transmitters (Holohil Systems, Ontario, Canada) weighed 3.3 g, had 25cm antennas, and had an operational life of at least

6 months. Signals were transmitted at frequencies between 150.018 and 150.991 MHz.

Fish were located weekly from 16 November 1995 to 11 December 1996 with a scanning receiver equipped with a directional antenna. To eliminate the possibility of tracking fish that had died or expelled transmitters, fish observed in the same position on successive sampling dates were visually located by wading. Upon locating a fish, we recorded the temperature, general habitat characteristics (pool, riffle, run), and association with structure.

We determined the accuracy of brown trout position data by locating hidden transmitters. The mean error associated with these locations was less than 3 m (N = 6), with a 95% confidence interval (CI) = 0.6-4.84 m. Therefore, only movements greater than 5 m were recorded. The positions of each fish were recorded on detailed maps and measured in relation to fixed reference points along the river corridor. Distances between reference points were determined either through direct measurement (<300 m) or by using a global positioning system (>300 m).

Position data for each fish were used to evaluate seasonal movement and activity and to estimate home range size. Seasons were defined as follows: winter (15 December-14 March), spring (15 March-14 June), summer (15 June-14 September), and fall (15 September-14 December). We defined movement as a detectable difference in position between consecutive samples, activity as the proportion (percent) of locations indicating movement within a season, and home range as the distance between the most upstream and downstream positions of an individual fish during a season. However, relatively large-scale unidirectional movements associated with spawning were not included in home range calculations or in calculations of activity and mean movement in fall. As a result of the large number of observations without detectable movement, we also calculated an adjusted mean movement, which included only nonzero values. We defined a shift in home range as occurring when a single long-distance movement interrupted multiple observations of consistent small-scale movements, resulting in a permanent displacement of a fish from one area to another. Thermal data recorders were used to record water temperature in the Chattooga River and East Fork from 5 April 1996 to 30 December 1996.

Seasonal differences in movement and home range were evaluated statistically using analysis of variance (ANOVA; $\alpha = 0.05$). Because multiple

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TABLE 1.—Mean total length, activity level, distance moved between consecutive locations, and home range for brown trout in the Chattooga River, by season. Values in parentheses are ranges. Activity refers to the percent of observations indicating movement from the previous position. The mean movement was computed from all observations, the adjusted movement from only those observations that indicated movement. Values within a column without a letter in common are significantly ($\alpha = 0.05$) different.

Season	Number of brown trout tracked	Mean ob- servations per fish	Total length (mm)	- Activity	Movement (m)		Home range
					Mean	Adjusted	(m)
Winter	5	11.8 (3–13)	285 (268–302)	31 z	20.5 z	67.4 zy	61.6 z (5–185)
Spring	14	8.9 (6–13)	289 (268–446)	13 y	6.8 y	53.0 zy	51.5 z (5–185)
Summer	12	6.7 (3–13)	282 (268–446)	17 y	4.5 y	27.7 z	27.7 z (5–80)
Fall	18	8.3 (3–13)	324 (268–435)	39 z	29.5 z	76.2 y	98.6 y (5-270)

positions were recorded for each brown trout during each season and some fish were tracked in more than one season, a mixed model of repeated measures was used in the statistical analyses, treating season as a fixed effect and fish and day as random effects. When a significant seasonal effect was detected, Fisher's least significant difference was used for comparison of group means generated from the mixed model. Analyses were performed with and without zero-movement observations. Seasonal differences in activity were analyzed using the chi-square statistic ($\alpha = 0.05$).

Results

Over a 52-week period, 414 individual day-time locations were collected for 27 brown trout (Table 1). Individual fish were observed over periods of 6-43 weeks. Data from four fish were collected in all four seasons, and data from an additional nine fish were collected during at least two seasons. A number of study fish made an apparent spawning migration in the fall. During a 2week period in November 1996, 8 of 18 study fish moved upstream an average of 2,091 m (range = 206-7,650 m). Six of these fish were observed building redds in gravel substrate in relatively shallow areas. Within a few days of spawning, 7 fish returned to their prespawning locations. The transmitter from the remaining fish was recovered from the substrate near the spawning location. No redd-building behavior was observed in nonmigrating fish. In order to eliminate bias, locations associated with presumed spawning migrations were removed from further statistical analyses of activity, movement, adjusted movement, and home range.

Brown trout exhibited strong site fidelity and

had small home ranges (Table 1). In all seasons, brown trout were generally found in association with structure in relatively deep water within a home pool. In winter, brown trout were found in riffles adjacent to the home pool in 20% of samples. In all other seasons, they were found in adjacent riffle habitat in no more than 5% of samples. Brown trout maintained a larger home range in winter than in all other seasons (F = 4.29, df = 48, P = 0.01). Individual home range size estimates were as high as 270 m. However, no individual movements independent of those associated with an assumed spawning migration exceeded 100 m (Figure 1). Movements to alternative locations within the home pool or to adjacent riffle areas were followed by a subsequent return to a preferred location within the home pool. Some fish were found in association with a single structure over periods as long as 30 weeks, resulting in an estimated home range size of 5 m, the resolution of our sampling technique. Although there were no barriers to movement within the study area, as evidenced by the spawning migrations observed in some fish, no fish moved through riffle habitat into adjacent pools during normal activity.

Chattooga River brown trout were significantly more active in winter than in spring ($\chi^2 = 10.3$, P < 0.001) and summer ($\chi^2 = 4.3$, P = 0.038; Table 1). Brown trout were also more active in fall than in spring ($\chi^2 = 27.6$, P < 0.001) and summer ($\chi^2 = 11.5$, P < 0.001). We did not detect a significant difference in activity between fall and winter ($\chi^2 = 1.2$, P = 0.266) or spring and summer ($\chi^2 = 1.3$, P = 0.248). On average, fish showed activity between consecutive samples on 39% of occasions in fall and 31% in winter, compared with

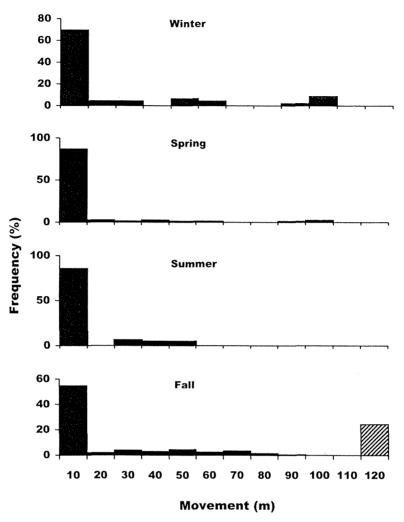


FIGURE 1.—Frequency distribution by season of weekly movements of brown trout in the Chattooga River. Crosshatched bar indicates movements associated with observed spawning activity.

only 13% in spring and 17% in summer. In addition to greater activity in fall and winter, brown trout also moved greater distances per movement during these seasons (F = 12.07, df = 377, P > 0.001; Table 1). On average, fish moved 29.5 m between consecutive samples in fall and 20.5 m in winter, compared with 6.8 m in spring and 4.5 m in summer. As differences in activity could affect the analysis, data were reevaluated considering only samples where movement was observed. Mean adjusted movement of brown trout was still significantly greater in fall than in summer (F = 5.06,df = 112, P = 0.003; however, no other seasonal differences were detected (Table 1). When movement was detected, brown trout moved an average of 27.7-76.2 m.

Seasonal water temperature ranges in the Chattooga River were as follows: 0-9°C in winter, 8-21°C in spring, 16-24°C in summer, and 7-16°C in fall. During summer, daily water temperatures in the Chattooga River exceeded 19°C over a consecutive period of 64 d, and daily minimum water temperatures remained higher than 19°C over an 18-d period. Although 5 fish were located in pools less than 500 m from a nearby tributary offering cooler temperatures (never exceeding 19°C), no fish moved from their established home ranges to exploit these lower water temperatures. During the 3 weeks subsequent to the period of continuous high water temperatures, transmitters from 6 of the 12 study fish were recovered from the riverbed.

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Discussion

During the day, adult brown trout in the Chattooga watershed were consistently found in small, well-established home ranges encompassing a single pool and the adjacent riffles. In all seasons, daytime locations of individual fish were restricted to a single pool or riffle—pool combination, and brown trout were routinely found in the same location over multiple sampling periods. Movements generally resulted in a change in location within the home pool to a location providing similar cover characteristics, which served as an alternative home site. Multiple home sites within well-defined home ranges have been observed for brown trout in other studies (Bachman 1984; Clapp et al. 1990; Young 1994).

We examined four brown trout recaptured 3-30 weeks after transmitter implantation and found that all incisions were healed and all fish had grown. Spawning migrations were also made by eight study fish. As in previous studies (Swanberg and Geist 1997; Bunnell et al. 1998), the presence of transmitters did not appear to alter behavior. Although no brown trout were confirmed to have died as a result of surgery, transmitters from 5 of 34 implanted fish were found within 1 week of implantation, strongly suggesting postsurgical mortality as the cause. An additional 12 transmitters were found more than 40 d after implantation, the result of expulsion, delayed mortality due to infection, or natural mortality. Although temperature may affect transmitter expulsion and infection rate in some species (Knights and Lasee 1996; Bunnell and Isely 1999; Walsh et al. 2000), most transmitters were lost after a period when water temperatures exceeded the upper avoidance temperature for brown trout of 19°C (Elliott 1975; Garrett and Bennett 1995) for an extended period. We believe the likely cause of transmitter loss was natural mortality associated with prolonged exposure to high temperatures. Although seemingly high, the proportion of transmitters lost in our study was similar to proportions reported in previous studies on brown trout (Meyers et al. 1992; Hudson 1993) and rainbow trout (Chisholm and Hubert 1985).

Brown trout were more active in the winter and fall than in the spring and summer and tended to move greater distances in the fall than in the summer, venturing farther into nearby riffle habitat. In a companion study, Bunnell et al. (1998) observed similar seasonal differences in the diel activity patterns of brown trout, noting that they move little

during the day, preferring to seek shelter in deep pools or near structure. Clapp et al. (1990) also noted the predominant use of cover in deep pools by brown trout during daylight hours. It is possible that the increased activity of brown trout in winter months with limited daylight hours incorporates crepuscular activity that was not observed in other seasons.

Summer water temperatures in the Chattooga River exceeded 19°C for an extended period; however, brown trout did not seek available thermal refuge in nearby tributaries. Although depth and possible groundwater intrusions may have buffered water temperatures in the pool habitat, the high assumed mortality of study fish after a prolonged period of high water temperatures suggests that water temperature may negatively influence brown trout populations in southern Appalachian streams. While optimal and preferred temperatures for brown trout vary between populations (Ferguson 1958; Coutant 1977; Reynolds and Casterlin 1979; Olson et al. 1988), water temperatures above 19°C can adversely affect growth (Elliott 1975) and angler catch rates (McMichael and Kaya 1991). Bachman (1984) noted that brown trout in a Pennsylvania limestone creek exhibited a lack of movement during summer. Whitworth and Strange (1983) found limited movement of brook and rainbow trout in southern Appalachian streams. Bunnell et al. (1998) found that diel movements in summer were significantly reduced relative to those in other seasons and suggested that this may have been the result of thermal stress. In other studies, however (Kaya et al. 1977; Garrett and Bennett 1995), similar temperatures have stimulated movements to cooler water in nearby tributaries. Seasonal habitat shifts have also been observed (Clapp et al. 1990; Meyers et al. 1992), but such shifts are generally associated with fall and winter spawning. These long-range upstream spawning migrations often result in a seasonal shift in home range to areas of lower water temperatures (Hudson 1993; Garrett and Bennett 1995). It is unclear why brown trout did not take advantage of cooler water in Chattooga River tributaries.

Brown trout spawning movements in the Chattooga River were confined to a relatively narrow time window in November. A maximum upstream movement during the spawning period of 7.65 km suggests Chattooga River brown trout are able to move long distances to reach spawning habitats, which is consistent with spawning migration distances for other brown trout populations (Meyers et al. 1992; Garrett and Bennett 1995). Brown trout

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exhibited strong site fidelity, returning to their original home ranges within a few days after spawning. Meyers et al. (1992) reported that brown trout rapidly moved long distances downstream shortly after spawning. Garrett and Bennett (1995) found a similarly rapid return to prespawning reservoir habitat in half of study fish but observed that the rest remained in tributaries near their spawning sites for extended periods. In contrast, Clapp et al. (1990) and Hudson (1993) noted that brown trout use separate ranges in summer and winter independently of spawning activity.

Almost half of all fall-tagged adult brown trout failed to make a spawning run. Although transmitter implantation may have affected reproduction, it is also possible that some Chattooga River brown trout lacked the energy or gonadal development necessary to spawn owing to stress caused by exposure to extended periods of high water temperatures in the summer. Brown trout in southern Appalachian rivers exhibit reduced growth in the summer (Ensign et al. 1990), possibly because of decreased food supplies (Cada et al. 1987). During this period of high water temperatures, energy intake levels may be below those necessary for maintenance metabolism, leaving no reserves for gamete growth. Kaya (1977) found that brown trout had significantly reduced reproductive success and gonadal formation when exposed to extended periods of high summer water temperatures. The effects of high summer water temperatures on southern Appalachian brown trout survival and reproductive success deserve further investigation.

Because brown trout have small, stable home ranges, managers may be tempted to implement regulations that favor small-scale area restrictions. The relatively long-range spawning migrations that we observed would suggest that more regional approaches to management are justified.

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